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In situ orientation of fish larvae can vary among regions

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ABSTRACT: Larval coral-reef fishes have good orientation abilities. Through-water orientation of larvae in some species is location-dependent at meso-scales <10s of km, whereas other species have location-independent orientation at meso-scales. *In situ* observation of the damselfish *Chromis atripectoralis* showed that settlement-stage larvae swam in a southerly direction (mean = 175 ± 11°) at 100 to 1000 m from shore, both east and west of Lizard Island, northern Great Barrier Reef (NGBR), in 10 datasets from 1998 to 2008. Wind direction did not directly influence through-water swimming direction at NGBR. During 2014, *in situ* diver observation tested if orientation of *C. atripectoralis* differed regionally in the central Great Barrier Reef (CGBR), 620 km south of NGBR, and in the New Caledonia reef lagoon (NCRL), 1950 km east of CGBR. In all 3 regions, >90% of larvae swam directionally with similar precision and speeds, and with significant among-individual orientation. Yet through-water orientation was easterly at CGBR (72 ± 30°) and NCRL (87 ± 20°), and significantly different from NGBR. Over-bottom orientation (i.e. the result of current and larval swimming), measured by GPS at start and end of observing each larva, was weak east-southeasterly at NGBR (116 ± 40°, p = 0.045), not significantly directional at CGBR, and strongly westerly at NCRL (246 ± 28°, p = 0.0006), indicating that dispersal of *C. atripectoralis* is both current- and behaviour-dependent. This is the first report of location-dependent larval fish orientation at a regional scale. This might be an evolutionary response to regional hydrodynamic conditions to limit downstream dispersal.

KEY WORDS: Connectivity · Dispersal · Larva · Orientation · Behaviour · Pomacentridae · Regional differences

INTRODUCTION

Pelagic marine waters are a challenging environment in which to achieve and maintain orientation. This is particularly true for larval stages of demersal animals that have only a short time to find appropriate shallow water habitat into which to settle once they become competent to settle (Arvedlund & Kavanagh 2009). These larvae are typically small, and their swimming structures and sensory systems may be incompletely developed. Pelagic larvae swim through water that is moving under both local (e.g. wind) and remote (e.g. the moon) physical drivers, and without a reference point outside this moving habitat, larvae would find it difficult to determine that they are being transported by currents, to say

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nothing of sensing the velocity (i.e. speed and direction) of the current. This makes orientation all the more difficult (Kingsford et al. 2002).

Yet it is clear that at least the larvae of reef fishes have not only good swimming abilities, but also the ability to orientate in the moving, pelagic ocean in a surprisingly precise way (Leis et al. 2011). A high percentage of individual pelagic larvae swim though the water with significant directionality, and significant among-individual orientation is common (Leis & Carson-Ewart 2003, Paris et al. 2013). Orientated swimming of larvae relative to moving water has been observed directly by following divers, and by the use of a drifting arena in which the behaviour of larvae can be filmed (Leis et al. 2014). Less common are *in situ* studies that combine water movement with the behaviour of the larvae to directly measure orientation and the net biophysical movement of larvae relative to the bottom.

Orientation of fish larvae *in situ* has typically been studied within a single region. Some studies have addressed spatial variation in orientation at meso-scales within a region; for example, on different sides of an island or peninsula (Stobutzki & Bellwood 1998, Hindell et al. 2003, Leis & Carson-Ewart 2003, Leis et al. 2006), inside a lagoon compared to the nearby open ocean (Leis & Carson-Ewart 2001), at different distances from the edge of a nearby reef (Leis & Carson-Ewart 2003), or in different water masses (Paris et al. 2013). Some species have location-specific orientation, which is typically interpreted as orientation in relation to a particular habitat (Leis et al. 2009, Paris et al. 2013); for example, swimming away from a reef during the day (Leis & Carson-Ewart 2003) or towards it at night (Stobutzki & Bellwood 1998). In contrast, other species demonstrate location-independent orientation at these meso spatial scales (Leis et al. 2014), indicating that a location-independent cue is used for orientation. However, it is not known if orientation in a species that demonstrates location-independent orientation at meso spatial scales might vary at larger scales among regions. It is important to know if larval orientation behaviour does vary spatially at regional scales for understanding and modelling larval dispersal.

To address the question of whether orientation by fish larvae varies among regions, we studied both through-water and over-bottom movement and orientation of settlement-stage larvae of a coral-reef damselfish, *Chromis atripectoralis*, that demonstrates consistent local location-independent orientation near Lizard Island in the northern Great Barrier Reef (NGBR). We did this in lagoonal habitats in 3 regions: Lizard Island (NGBR), Big Broadhurst Reef off Townsville in the central Great Barrier Reef (CGBR), and Larégnère Reef off Noumea in the southwest reef lagoon of New Caledonia (NCRL). Approximate distances between these regions are 620 km (NGBR–CGBR), 1950 km (CGBR–NCRL) and 2400 km (NGBR–NCRL). At NGBR, data are available from previous studies over a 10 yr period, on both sides of Lizard Island, and at distances of 100 to 1000 m from the reef edge. These data were analyzed by Leis et al. (2014), and show consistent orientation behaviour (swimming to the south) at all spatial and temporal scales examined. Our studies at the other 2 locations (reported here) are much less extensive, but allowed us to test whether the consistent orientation behaviour found at NGBR is also evident in other regions.

MATERIALS AND METHODS

Study locations

The orientation of larvae was studied in 3 regions (Fig. 1A): (1) NGBR, 100 to 1000 m off the fringing reef edge both east and west of Lizard Island, Great Barrier Reef (14° 40′ S, 145° 27′ E; Fig. 1B), over a sandy bottom of 10 to 35 m depth. Observations were made from November to February 1998 to 2008 (i.e. late Austral spring and summer) between 08:25 and 18:05 h under a variety of wind conditions (see Leis et al. 2014). (2) CGBR, 100 to 500 m off the NW side of Big Broadhurst Reef (18° 53′ S, 147° 42′ E; Fig. 1C) in an area that shoaled from ca. 30 to 15 m, with scattered coral heads of various sizes on a sandy bottom in the shallower areas (a typical back-reef environment). Observations were made 2 to 8 February 2014 between 08:50 and 16:15 h, and winds were from the E to ESE at 12 to 30 knots (22 to 55 km h^{-1}). Weather conditions prevented work off the east side of the reef. (3) NCRL, 150 to 1200 m off both the north and south sides of Larégnère Reef (22° 20′ S, 166° 19′ E, Fig. 1D) over a largely sandy bottom of 10 to 18 m depth (a few small, isolated coral heads were encountered north of the reef, and some areas of hard bottom were present south of the reef). Observations were made between 23 November and 1 December 2014 at 08:30 to 14:20 h, and winds were from the E to ESE at 12 to 28 knots (22 to 52 km h^{-1}).

In each region, the study area was near a mid-shelf reef within the lagoon of the barrier reef system (Fig. 1). At both NGBR and CGBR, water temperatures were between 28 and 30°C, whereas at NCRL they were 24 to 26°C. The shallow depths and clear

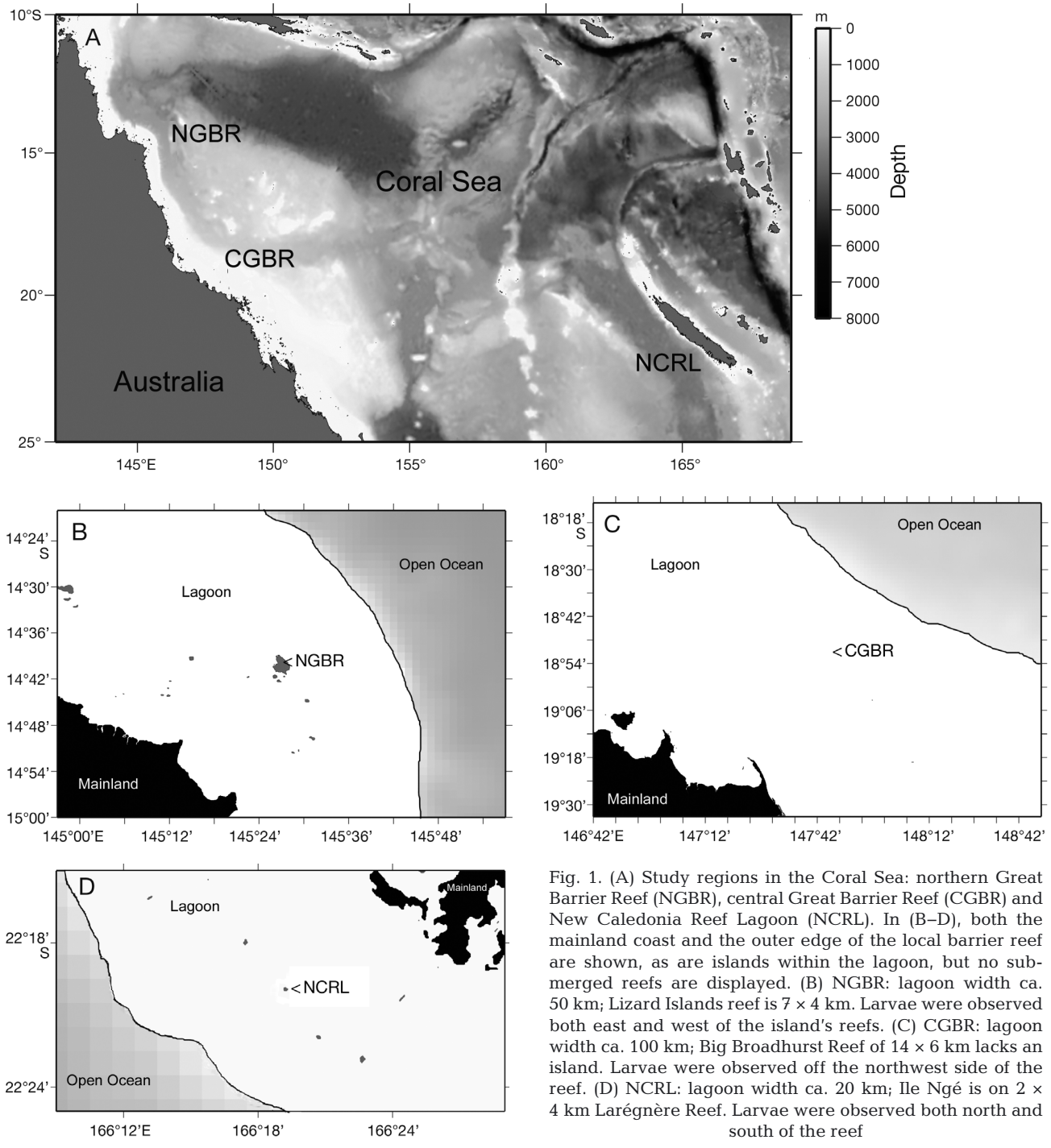

Fig. 1. (A) Study regions in the Coral Sea: northern Great Barrier Reef (NGBR), central Great Barrier Reef (CGBR) and New Caledonia Reef Lagoon (NCRL). In (B–D), both the mainland coast and the outer edge of the local barrier reef are shown, as are islands within the lagoon, but no submerged reefs are displayed. (B) NGBR: lagoon width ca. 50 km; Lizard Islands reef is 7 × 4 km. Larvae were observed both east and west of the island's reefs. (C) CGBR: lagoon width ca. 100 km; Big Broadhurst Reef of 14 × 6 km lacks an island. Larvae were observed off the northwest side of the reef. (D) NCRL: lagoon width ca. 20 km; Ile Ngé is on 2 × 4 km Larégnère Reef. Larvae were observed both north and south of the reef

waters of the lagoon study areas ensured that the larvae could readily be observed in the same environment in which they were captured by light traps only a few hours before. Magnetic declination differs among the 3 regions (NGBR: 6.5°, CGBR: 7.7°, NCRL: 12.1°), so compass bearings were corrected to provide bearings in degrees true.

Study species

The study species in all regions was the pomacentrid damselfish *Chromis atripectoralis* Welander & Schultz, 1951. Size of *C. atripectoralis* at settlement (and hence size of the larvae studied here) is 7 to 10 mm standard length (SL). This species has a

pelagic larval duration (PLD) of 10 to 24 d (mean 16 d; Wellington & Victor 1989, Bay et al. 2006a). Larvae were captured in light traps 50 to 100 m off the reef edge, and observed *in situ* on the day of capture. Between capture and *in situ* observation, the larvae were kept in covered 15 l buckets, with frequent changes of sea water that was obtained from the surrounding pelagic waters where the larvae had been captured.

Field methods

Larvae were observed *in situ* using the 'following methodology' as described in previous publications (especially Leis et al. 1996, Leis & Carson-Ewart 1997, 1998). Briefly, 2 divers took a larva in a small container to a depth of 5 m, and faced in a random direction. The larva was then released by the divers who followed it at 1 to 2 m distance, and recorded depth (with 0.1 m precision) and bearing (degrees magnetic to nearest 5°) at 30 s intervals, and distance travelled using a calibrated plankton-net flow meter, from which speed was calculated. One dataset from NGBR was from groups of ca. 10 larvae released at a time. Observation runs typically lasted 10 min, providing 21 measures of swimming direction, after which the larvae were allowed to swim away. Within-individual statistics refer to these 21 observations. Some runs were shorter if the larvae were lost or descended below our safety depth, but are included in the analysis if they lasted more than 2 min (>5 observations). Among-individual statistics refer to the distribution of mean bearings from replicate observations of individual larvae. This methodology provides a measure of swimming velocity (i.e. direction and speed) relative to the water, which is itself usually moving. Diver-following of larvae allowed observation and quantification of behaviour *in situ*, where the larvae are subject to the full range of cues and other natural influences in their environment, as opposed to studies of behaviour in the laboratory. A more detailed discussion of the diver-following methodology and the validity of the data it provides are found in the Supplement at www.int-res.com/articles/suppl/m537p191_supp.pdf.

We also measured movement of the larvae relative to the bottom by use of a GPS position fix at the start and end of following each larva: i.e. from when the divers left the surface before the observation run to when they returned to the surface after the run. The distance and direction travelled were used with the elapsed time to determine speed and direction relative to the bottom (over-bottom). This is a less precise measure of velocity than that obtained from following through the water, because it includes the time before and after the following-run during which the divers were descending and ascending. For this reason, only runs that were at least 5 min in duration were included to minimize the relative effect of the movement of the divers by currents during decent and ascent.

Observations of larval behaviour over a period of 10 min were sufficient to satisfy statistical requirements and for comparisons among locations, times and regions. We do not know if the directionality of an individual larva observed for 10 min would differ from that measured over a longer period of time. Measurements made over longer periods might conceivably provide different results, but addressing this possibility would require the use of other methods (for example, the drifting *in situ* chamber; Paris et al. 2008).

Data analysis

Circular statistics were used to analyze directional data (See Zar 1996 for details) and were done largely with Oriana software (Kovach Computing Services), including calculating mean bearing and 95% confidence interval (95% CI) of the mean bearing, directional precision (length of the mean vector, r, which varies from 0 to 1, the latter indicating all bearings are the same; r is unitless), Rayleigh tests (R-test) for single sample tests for uniformity of the distribution of angles, Watson U2 test (WU2 test) for multiple sample tests for differences in distribution of bearings. In all tests, results were considered significant at $p < 0.05$. No correction for multiple testing was attempted, rather, we provide actual p-values to allow the reader to assess if a Type I error due to multiple testing was likely.

For each run, the mean bearing was computed and its significance assessed with R-tests. Significant runs are said to be directional. Only significant, within-individual directional means were used in among-individual (second-order) analyses to assess the overall among-individual orientation within each dataset (R-test) and for comparisons between datasets (WU2 test). Thus, the questions asked were: for individuals with significant within-individual directionality, is there significant among-individual orientation, and does among-individual orientation of directional larvae differ among datasets? In our previous studies, the majority (typically >90%) of larvae

Table 1. Through-water directionality (within-individual) and orientation (among-individual) of *Chromis atripectoralis* larvae in 3 regions. NGBR: northern Great Barrier Reef; CGBR: central Great Barrier Reef; NCRL: New Caledonia Reef Lagoon. Significant orientation is indicated by an among-individual p-value of <0.05. Range of speeds at NGBR is from the 10 datasets listed in Table 3 (see Leis et al. 2014)

Region	No. observed	Within-individual median length of mean vector (r)	No. with significant within-individual directionality (%)	Among-individual mean bearing ±95% CI (in degrees true)	Among-individual length of mean vector (r)	p-value (from R-test)	Mean speed (cm s^{-1})
NGBR	278	0.88	260 (93.5)	175 ± 11°	0.41	<<0.0001	21.6–30.0
CGBR	44	0.84	40 (90.9)	72 ± 30°	0.40	0.002	31.6
NCRL	68	0.81	62 (91.2)	87 ± 20°	0.48	<<0.0001	23.6

Table 2. Comparison of through-water orientation of *Chromis atripectoralis* larvae on opposite sides of reefs in 2 regions. NGBR: northern Great Barrier Reef; NCRL: New Caledonia Reef Lagoon. NGBR after Leis & Carson-Ewart (2003), and includes only observations made in the morning because no afternoon observations were available from the east side of the island

Region/side	n	Among-individual mean bearing ±95% CI (in degrees true)	Among-individual length of mean vector (r)	p-value (from R-test)	WU2 test:windward vs. leeward side of reef
NGBR windward (east)	39	157 ± 25°	0.48	<0.0001	>0.10
NGBR leeward (west)	42	149 ± 19°	0.58	<0.0001	
NCRL windward (southeast)	13	97 ± 85°	0.31	0.29	>0.05
NCRL leeward (northwest)	49	85 ± 25°	0.52	<<0.0001	

exhibited significant within-individual directionality (e.g. Leis et al. 2014).

To test whether wind direction might directly influence the orientation of larvae, we used the NGBR data on *C. atripectoralis* from Leis & Carson-Ewart (2003). This consisted of observations of 88 larvae taken 100 to 1000 m off the reef edge over several years in a variety of wind conditions, and was the most extensive dataset available for which wind direction was not essentially consistent throughout. Field notes were used to partition the orientation data among 3 main wind conditions (other conditions were too rare for testing): southerly wind (S to SE, n = 53), northerly wind (N to NW, n = 18), and light, variable wind (n = 8). The resulting 79 mean swimming directions were used to test the hypothesis that swimming direction did not vary among the 3 wind conditions. Data from east and west of the island were tested separately, and also when pooled. First, a second-order analysis was performed for each part of the partitioned data using the R-test to determine if there was significant among-individual orientation under those wind conditions. We then used the WU2 test to determine if the distribution of swim directions differed significantly among wind conditions. The meteorological convention was used for wind direction (i.e. the direction from which the wind was blowing). In contrast, the oceanographic convention was used for current direction (i.e. the direction toward which the current was flowing).

RESULTS

Orientation through the water

The number of larvae observed ranged from 44 at CGBR to 278 at NGBR. In each region, 82 to 86% of individuals were observed for a full 10 min, and more than 90% of individuals exhibited significant swimming directionality (Table 1). Median within-individual directional precision ranged from r = 0.81 to 0.88 in the 3 regions. Mean swimming speed through the water ranged from 21.6 to 31.6 cm s^{-1}, depending on location and which of the 10 NGBR datasets was selected (Table 1). In each region, the larvae were on average vertically positioned in the upper half of the water column, with mean swimming depths of 4.2 m at NCRL, 7.1 m at CGBR and (depending on location) 5 to 12 m at NGBR (Leis 2004).

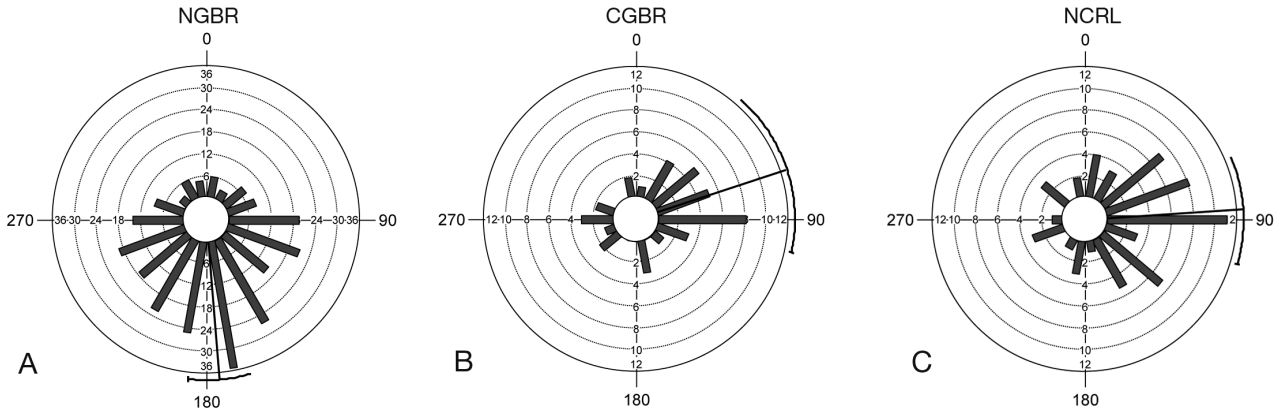

Fig. 2. Frequency distribution of through-water mean bearings of *Chromis atripectoralis* larvae in 3 regions. The radius is the mean bearing; the arc outside the circle represents the 95% CI. p-values are from the R-test. (A) NGBR: northern Great Barrier Reef. Mean bearing = 175 ± 11° (r = 0.41, p << 0.0001, n = 260); (B) CGBR: central Great Barrier Reef. Mean bearing = 72 ± 30° (r = 0.40, p = 0.002, n = 40); (C) NCRL: New Caledonia Reef Lagoon. Mean bearing = 87 ± 20° (r = 0.48, p << 0.0001, n = 62)

Within-region orientation

We tested whether orientation (i.e. swimming direction through the water) differed between 2 sides of the study reef (i.e. the nominal windward and leeward sides) for NGBR and NCRL, and in both cases the WU2 test detected no difference in orientation between the 2 sides (Table 2). Therefore in further testing, data from both sides of the reef were pooled. At CGBR, we obtained data from only one side of the reef (i.e. the western, leeward side).

Regional orientation (Fig. 2, Table 1)

In all 3 regions, the larvae exhibited strong among-individual orientation, with precision ranging from r = 0.40 to 0.48. At NGBR, the mean bearing (±95% CI) was to the south (175 ± 11°), and was also southerly in 10 datasets recorded over a 10 yr period (Table 1). In contrast, at the other 2 regions the mean bearing was to the east: 72 ± 30° at CGBR, and 87 ± 20° at NCRL. The distribution of bearings at NGBR differed significantly from that in the other 2 regions (WU2 tests, $p < 0.001$), whereas CGBR and NCRL did not differ significantly from each other (WU2 tests, $p > 0.5$). When the 10 datasets that made up the pooled NGBR data mentioned above were tested individually, only 2 were not significantly different from the CGBR and NCRL data (Table 3). These 2 datasets (CFE2 and CFW2 in Table 3) were from an experiment in which underwater sounds were broadcast while orientation was observed (Leis et al. 2002). In both, recordings of reef noise were broadcast, and although mean direction was to the south, no significant among-individual orientation was found. In the third NGBR dataset from the same experiment, 'white noise' was broadcast (CFW4 in Table 3); significant orientation to the south was found which was significantly different from orientation at CGBR and NCRL. No underwater sounds were broadcast during observations at CGBR or NCRL.

Table 3. Comparison of among-individual orientation of *Chromis atripectoralis* larvae among 3 regions. NGBR: northern Great Barrier Reef; CGBR: central Great Barrier Reef; NCRL: New Caledonia Reef Lagoon. For NGBR, data sets collected at different times are also compared individually to CGBR and NCRL: CF codes for NGBR refer to different datasets identified as per Leis et al. (2014). CFE2 and CFW3 are datasets where underwater sound was broadcast while the larvae were being observed *in situ* (Leis et al. 2002); neither had significant among-individual orientation. n: number of larvae with significant within-individual directionality; ns: not significant

	CGBR (2014) WU2 test (p)	NCRL (2014) WU2 test (p)	n	Date
NGBR all data	<0.001	<0.001	260	1998–2008
NGBR–CFE1	<0.001	<0.001	39	1998–1999
NGBR–CFE2	0.1 > p > 0.05 (ns)	<0.01	15	1999
NGBR–CFE3	<0.002	<0.001	20	2008
NGBR–CFW1	<0.001	<0.001	42	1998–2000
NGBR–CFW2	<0.001	<0.001	41	1999–2000
NGBR–CFW3	0.2 > p > 0.1 (ns)	0.2 > p > 0.1 (ns)	19	1999
NGBR–CFW4	<0.001	<0.001	23	2001
NGBR–CFW5	<0.001	<0.001	9	2008
NGBR–CFW6	<0.01	<0.05	17	2008
NGBR–CFW7	<0.001	<0.001	35	2008
CGBR	–	>0.5 (ns)	40	2014
NCRL	>0.5 (ns)	–	62	2014

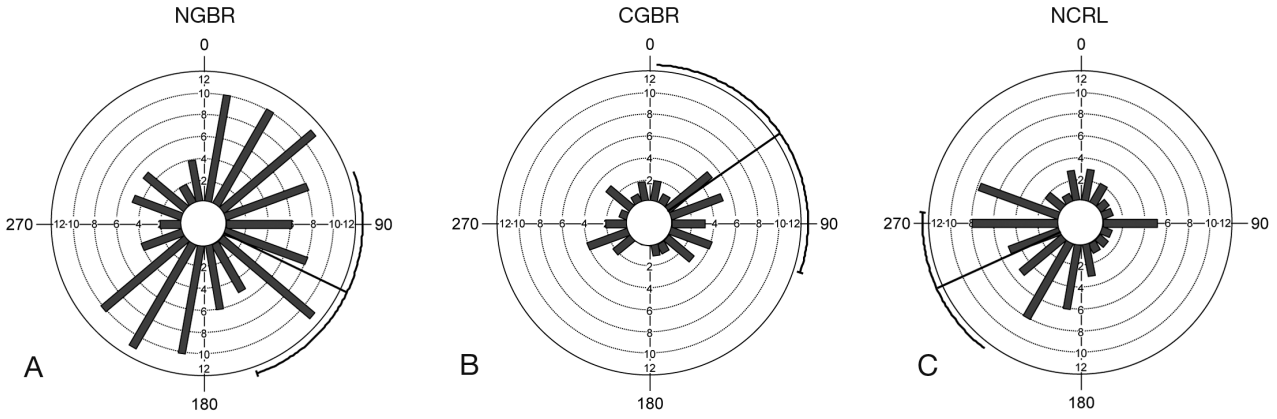

Fig. 3. Frequency distribution of over-bottom mean bearings of *Chromis atripectoralis* larvae in 3 regions. p-values are from the R-test. (A) NGBR: northern Great Barrier Reef Lagoon. Mean bearing = 116 ± 40° (r = 0.16, p = 0.045, n = 128); (B) CGBR: central Great Barrier Reef Lagoon. Mean bearing = 55 ± 55° (r = 0.24, p = 0.11, n = 40); (C) NCRL: New Caledonia Reef Lagoon. Mean bearing = 246 ± 28° (r = 0.34, p = 0.0006, n = 64)

Table 4. Net over-bottom movement of *Chromis atripectoralis* larvae in 3 regions. NGBR: northern Great Barrier Reef; CGBR: central Great Barrier Reef; NCRL: New Caledonia Reef Lagoon. NGBR data are from the study of Leis & Carson-Ewart (2003) (datasets CFE 1, CFW1 and CFW2 in Table 1)

Region	n	Direction of net over-bottom movement (Mean ± 95% CI)	Length of mean (r) vector of net over-bottom movement	p-value (from R-test)	Mean net over-bottom speed (cm s^{-1})
NGBR	128	116 ± 45°	0.16	0.045	17.7
CGBR	40	55 ± 28°	0.24	0.11	25.9
NCRL	64	246 ± 28°	0.34	0.0006	20.5

Orientation relative to the bottom (over-bottom orientation; Fig. 3, Table 4)

At NGBR, the direction of the among-individual net over-bottom movement was just significant with a mean bearing to the ESE (mean = 116 ± 45°, R-test, r = 0.16, p = 0.045, n = 128). Here, the general north–south movement of the tidal current combined with the generally S–SE swimming of the larvae resulted in a weak net movement to the ESE. Precision was low (r = 0.16), and the marginal significance is due only to the high power provided by very large sample size. There was no significant difference in the distribution of over-bottom bearings between east and west sides of the island (WU2 test, $p > 0.20$, $n_{east} = 40$, $n_{west} = 88$).

At CGBR, the among-individual net over-bottom movement was to the NE (55°), although this was not significant (R-test, r = 0.24, p = 0.11, n = 40). In this region, it appears that the north–south movement of the tidal current (directed by reef topography) dominated, and that, combined with the easterly swimming of the larvae, resulted in no overall directional significance.

At NCRL, among-individual net over-bottom movement was highly significantly orientated (R-test, p = 0.0006) to the W–SW (246 ± 28°, r = 0.34, n = 64). So even though the average swimming direction of the larvae through the water was to the east, the strong current moved the larvae on average to the west. In this location during our study, there was no strong diel change in current direction due to tide, with the strong easterly wind during the study helping to keep the water moving to the west, taking the larvae in that direction. In this region, there was a significant (p = 0.005) negative correlation between net over-bottom speed, and the difference between the through-water direction and the over-bottom direction (Fig. 4), although this explained only 12% of the variation in over-bottom speed. In other words, the rate of displacement of the larvae was reduced when the larvae swam into the current, and increased when they swam with the current.

Effect of wind on orientation

There was no clear indication that wind direction directly influenced swimming orientation at NGBR, the only region for which we had data suitable for testing. The north vs. south wind contrast was the most powerful test because it had the highest num-

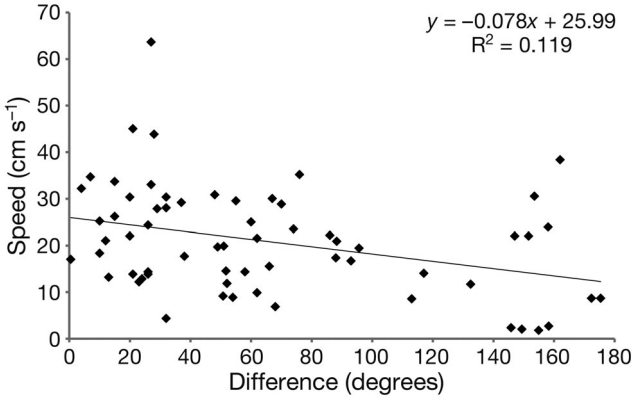

Fig. 4. Relationship between the difference (in degrees) between the over-bottom bearing and through-water bearing vs. the over-bottom speed (cm s^{-1}) of *Chromis atripectoralis* larvae at NCRL (New Caledonia Reef Lagoon). (p = 0.005, n = 64)

ber of replicates. It is also where one would expect to find a wind direction effect (if one did exist), because the 2 wind directions are as different as is possible. At NGBR, through-water orientation of larvae when the wind was from the north did not differ from when the wind was from the south: none of the north wind vs. south wind tests returned a significant difference in larval orientation between these 2 wind conditions (WU2 test, $p > 0.5$; Table 5, Fig. 5). Under both north and south wind, the larvae swam to the south (mean bearing 133 to 188° depending on side of island and wind direction, and 166 vs. 142° with both locations pooled, with no significant differences found; Table 5).

In contrast, when orientation under light variable winds was compared with that from either north or south winds, a significant difference was found in some cases, with a more easterly mean bearing (120°) under light variable winds (Table 5, Fig. 5). But the results are ambiguous, in part because orientation data under light variable winds were only available from off the east side of the island, and replication was low. If the comparison is limited to the east side of the island, a significant difference in mean orientation was found between light variable conditions and southerly winds (with orientation under the former more easterly: WU2 test, $p < 0.02$; Table 5), but not with northerly winds (WU2 test, $0.2 > p > 0.1$, most likely due to low replication). With data from both sides of the island pooled, a difference that approaches significance was found, but only between light, variable conditions and northerly winds (WU2 test, $0.1 > p > 0.05$; Table 5), not southerly winds (WU2 test, $0.2 > p > 0.1$). For this reason, and because of the low number of observations with light variable winds, this apparent difference must be regarded with caution.

It is noteworthy that when similar analyses were performed with data for larvae of 3 other species (2 pomacentrids and a chaetodontid) from the same study (Leis & Carson-Ewart 2003), no significant differences in orientation among wind directions were found, including for light variable conditions (authors' unpubl. data). Therefore we conclude that wind direction had little, if any, direct influence on the through-water swimming direction of *C. atripectoralis* larvae. There is equivocal evidence, however, that wind conditions (e.g. light variable winds) as opposed to wind direction per se, might have an influence.

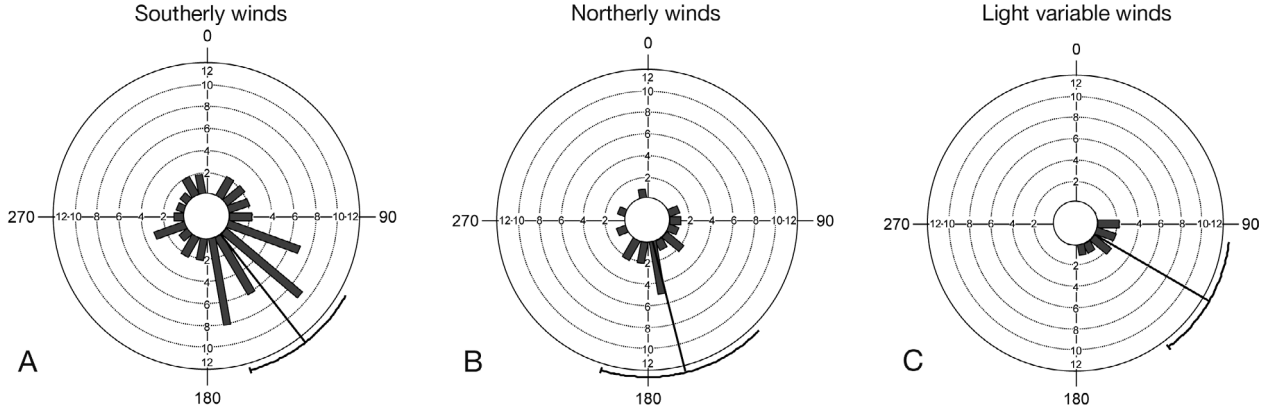

Fig. 5. Frequency distribution of through-water mean bearings of *Chromis atripectoralis* larvae under different wind conditions at northern Great Barrier Reef Lagoon (NGBR) (see Table 5). p-values are from the R-test. (A) Southerly winds. Mean bearing = 142 ± 22° (r = 0.46, p < 0.0001, n = 53); (B) northerly winds. Mean bearing = 166 ± 32° (r = 0.55, p = 0.003, n = 18); (C) light variable winds. Mean bearing = 120 ± 23° (r = 0.90, p = 0.00024, n = 8)

Table 5. Comparison of through-water swimming directions of *Chromis atripectoralis* larvae under different wind conditions at northern Great Barrier Reef (NGBR; data from the study of Leis & Carson-Ewart 2003). Length of the mean vector, r, is a measure of orientation precision. Data were available from the east and west sides of Lizard Island, and are tested for each side separately and both sides pooled. The number of observations (3) for northerly wind conditions on the west side of the island was too low for the WU2 test. The only WU2 test that returned a significant result was for the east side of the island, when southerly wind was compared to light variable wind. NA: not applicable

Wind: / Side of island:	Southerly East	Northerly East	Light, variable East	Southerly West	Northerly West	Southerly Both sides	Northerly Both sides
No. of observations	11	15	8	42	3	53	18
Mean bearing ± 95% CI	188 ± 63°	165 ± 50°	120 ± 23°	133 ± 22°	169 ± 8°	142 ± 22°	166 ± 32°
r	0.41	0.46	0.9	0.51	0.99	0.46	0.55
p-value (from R-test)	0.15	0.041	0.0002	<<0.0001	0.03	<0.0001	0.003
WU2 tests		p (WU2)	p (WU2)	p (WU2)	p (WU2)	p (WU2)	p (WU2)
Southerly wind/east side	–	>0.5	<0.02	NA	n too low	NA	NA
Northerly wind/east side		–	0.2 > p > 0.1	>0.5	n too low	NA	NA
Light, variable wind/east side			–	0.5 > p > 0.2	n too low	0.2 > p > 0.1	0.1 > p > 0.05
Southerly wind/west side				–	n too low	NA	NA
Northerly wind/west sides					–	NA	NA
Southerly wind/both sides						–	>0.5

DISCUSSION

Using larval-following methodology, we found that *Chromis atripectoralis* exhibited remarkably consistent orientation behaviour in the vicinity of Lizard Island in the NGBR. Its settlement-stage larvae orientated to the south on both the east (windward) and west (leeward) sides of the island, and at varying distances from shore. Not only was the orientation of *C. atripectoralis* at Lizard Island consistent at meso spatial scales, it was also consistent at temporal scales over 10 yr (Leis & Carson-Ewart 2003, Leis et al. 2014). On a diurnal scale, orientation was somewhat more easterly in the morning and more westerly in the late afternoon (Leis et al. 2014), but mean orientation was always southerly. There was little indication from the Lizard Island data that wind direction had a direct influence on through-water orientation, although further study of this possibility is warranted. Further, orientation of *C. atripectoralis* larvae at Lizard Island did not differ when an alternative method (the DISC, or Drifting *In Situ* Chamber; Paris et al. 2008) was used to measure it (Leis et al. 2014), thus corroborating the larval-following results.

The studies at both CGBR and NCRL were much less extensive, but provided results that were consistent with those from NGBR with one important difference: among-individual mean orientation. In all 3 regions, 91 to 94% of individuals swam through the water directionally, with similar within-individual precision (median r = 0.81 to 0.88). Significant among-individual orientation was also found in all 3 regions, with similar among-individual precision (r = 0.40 to 0.48). In the 2 regions where comparisons between 2 sides of the study reef were possible (NGBR and NCRL), no significant difference in orientation was found. However, as noted above, the mean among-individual through-water bearing was not the same in the 3 regions. This suggests an adaption to local currents to minimize dispersion and transport, as suggested by Mouritsen et al. (2013) for larvae of a different species in a southern Great Barrier Reef location. Mouritsen et al. (2013) tested for sun compass orientation by measuring orientation of apogonid larvae ashore in basins (17 cm diam.) with limited possible orientation cues and constrained physical and biological conditions, but they did not consider possible regional differences in orientation. We measured orientation of pomacentrid larvae *in situ* in near-reef waters with a full range of ambient cues and conditions present, and the orientation we documented varied among regions. We did not, however, test for any specific cues involved in that orientation, and the orientation differences we documented here could be due to cues other than what we consider below.

We cannot be certain that the differences among regions in through-water orientation we found would persist over time, but the temporal consistency of orientation over 10 yr at NGBR indicate that they would. So, in larvae of *C. atripectoralis*, there seems to be spatial consistency in orientation at scales up to about 10 km, but not at 100s to 1000s of km. At what spatial scale orientation of *C. atripectoralis* larvae changes from being location-independent to loca-

tion-dependent is a question requiring further research.

The purpose of our study was to determine if orientation of larvae varied among regions, and we found that it did. We did not set out to determine why orientation might differ, but based on our results, we can suggest some reasons, and eliminate others.

There was little indication that the larvae were responding to cues emanating from the nearest reef and attempting to reach it. At NGBR, larvae on the west (leeward) side of the island swam on average toward the island's reefs, but those on the east (windward) side of the island swam on average away from the island. At CGBR, where we had observations from only the reef's west side, the larvae swam toward the reef. At NCRL, the larvae on both the north and south sides of the reef had an average swimming direction parallel to the reef. This, plus the location-independent orientation of *C. atripectoralis* at meso-scales strongly suggest that reef-based cues were not being used by the larvae for orientation.

At both CGBR and NCRL, the ENE to E through-water orientation of the larvae and the consistent E to ESE wind during the study suggests that the larvae might be responding to the wind by swimming toward the direction from which it was blowing. Given the water clarity and depths involved in our *in situ* observations, and the vertical position of the larvae in the upper half of the water column, it is relatively simple for a human diver to determine the wind direction by looking upward at the surface to observe the direction of movement and breaking of wind-driven surface waves (authors' pers. obs.). Waves viewed from below the water appear as a pattern of alternating bright and dark bands providing large-scale, high contrast visual cues. This pattern is likely to be detectable by the larvae, as *in situ* observations of the distance at which fish larvae react to predators and reef habitats indicate they can detect and respond to objects at a distance of at least 6 to 10 m (Leis & Carson-Ewart 2001, 2002), and estimations of their resolving power (a measure of acuity based on photoreceptor spacing) indicate that settlement-stage larvae can detect a 30 cm object from a distance of 12 to 30 m given sufficient contrast (Lara 2001). However at Lizard Island, there was no significant difference in through-water swimming orientation between northerly and southerly winds, indicating that wind direction does not directly influence larval swimming direction. Similarly, a study on orientation of lobster larvae did not find a consistent orientation behaviour relative to wind direction, with the larvae at times swimming approximately downwind, while at others swimming approximately upwind (Kough et al. 2014). In spite of this, it must be noted that in lagoons of coral reefs, wind direction and speed strongly influence current speed and direction (Frith et al. 1986, Cuif et al. 2014), so indirect wind influence via wind-driven currents is possible if the larvae are responding to real-time current.

Although larvae could conceivably be responding to the real-time current, and for example, swim into the real-time current (which would tend to minimize dispersal), there is no clear evidence that they do this. Given the water clarity, bottom depths and swimming depths of the larvae in the study areas, it is often (but not always) possible for human divers to see the bottom in most locations, but seldom off the deeper east side of the reef at NGBR (authors' pers. obs.). A view of the bottom can provide the necessary external reference point that might allow larvae to determine the direction of the current, particularly if the larva drifted with the current for a time to assess this rather than swimming constantly. Alternatively, if a larva swam to attempt to maintain a fixed position relative to the bottom, it would be swimming into the current. Given the net movement of the larvae relative to the bottom and their swimming orientation through the water at NGBR and CGBR, where strong tidal reversals in current direction were present (Frith et al. 1986, authors' pers. obs.), it is clear that larvae were not swimming into the real-time current any more frequently than in any other direction relative to the current. At NCRL, the flow is strongly dominated by wind-induced current, which is an order of magnitude stronger than the tidal currents (Douillet 2001, Cuif et al. 2014), and the wind (i.e. the trade wind) was consistently from only one direction during our study. So, although the NCRL larvae did on average swim into the current direction, the relative lack of variation in current direction makes this weak evidence for there being a response to the real-time current. In spite of this, we found that swimming into the current at NCRL resulted in slower down-stream displacement than swimming with the current. Although this is exactly what one would expect, it is the first explicit demonstration that marine fish larvae can, indeed, minimize down-stream dispersal by horizontal swimming. It is important to keep in mind that although the larvae do swim in a highly orientated manner, they do not necessarily swim in a straight line at the speeds we measured. Rather, the median length of the mean vector of ca. 0.8 to 0.9 indicates that net through-water speed of individual larvae in the direction of travel was 10 to 20% slower than the reported through-water speed.

All 3 study sites were located in continental shelf coral-reef lagoons facing the Coral Sea. Yet the currents differ among these regions (GBR based on surface drifters and moored current meters, NCRL based on a validated hydrodynamic model). At NGBR, the mean non-tidal current is to the north (Frith et al. 1986, Choukroun et al. 2010). At CGBR, the mean non-tidal current is to the west (Choukroun et al. 2010, S. Choukroun, pers. comm., based on a nearby IMOS current-meter mooring). At NCRL, the current is to the W to NW, and is dominated by wind-forcing, which during the spring/summer spawning season is on average from about 120° (Douillet 2001, Cuif et al. 2014). In particular, in the vicinity of the study area near Larégnère Reef, the current under easterly winds is consistently to the west (i.e. downwind), although the complex reef topography within the lagoon means local variations from this westerly flow occur elsewhere in the lagoon (Douillet 2001). In the GBR study sites, tidal currents are strong but largely reversing, with little net tidal transport (Frith et al. 1986), whereas at NCRL the tidal currents are an order of magnitude less than the wind-driven currents, and as a result, net currents change little in direction over the tidal cycle when winds are strong, as they are during most of the spring/summer reef-fish spawning season (Cuif et al. 2014).

The among-individual swimming orientation of the larvae in each study area (S in NGBR, E in CGBR and NCRL) is directly into the long-term average (non-tidal) current in that region (to the N in NGBR, and to the W in CGBR and NCRL). This behaviour would tend to minimize downstream dispersal of larvae in each area. This is not a behavioural response to the real-time current, as the current varies with the tide (at least on the GBR), and at the CGBR study area, is topographically directed in a direction that differs from the long-term average in the region.

This 180° difference between swimming direction and current direction might seem to require behaviour that is genetically influenced to suit local hydrographic conditions: that is, an evolutionary response. Genetic differences on spatial scales similar to or smaller than the 600 to 2400 km considered here have been found in several species of *Chromis*, including *C. atripectoralis*, thus making this a reasonable expectation. Genetic differences between populations of *C. atripectoralis* were found between the northern and southern GBR, 1000 km apart in 2 studies (Doherty et al. 1995, Bay et al. 2006b). Similarly, in Hawaii, populations *Chromis verater* on reefs 50 to 200 km apart differed genetically (Tenggardjaja et al. 2014), *Chromis ovalis* had 'multiple significant genetic breaks' across the 2500 km long Hawaiian Archipelago (Tenggardjaja et al. 2012), and in the Mediterranean, a 'genetic break' was found between populations of *Chromis chromis* about 750 km apart (Domingues et al. 2005). Clearly, it would be of interest to determine if there were genetic differences in *C. atripectoralis* populations among the 3 study regions.

A possible alternative explanation is that larvae not having the orientation behaviour documented here would be dispersed downstream, leaving within the study areas only those larvae that swam into the long-term current. This could eventually lead to development of genetic differences among populations, especially if the behaviour was consistent over the full PLD. The ontogeny of orientation behaviour in larvae of *C. atripectoralis* has not been studied, so we do not know if the orientation behaviour of settlement-stage larvae occurs in younger larvae. It might only apply to larvae competent to settle, as ontogenetic changes in orientation behaviour have been found in larvae of other marine fish species (Leis 2010).

Further research is required to address these possibilities, but we think the hypothesis that *C. atripectoralis* larvae are swimming into the long-term current direction is the most likely explanation of the orientation behaviour we documented here. In any case, a question arises about the cues that might be used by the larvae to achieve orientation that is location-independent on meso-scales, but regionally dependent. A celestial cue is one possibility. There are indications that *C. atripectoralis* larvae use a sun compass (Leis & Carson-Ewart 2003, Leis et al. 2014), and the use of celestial cues for orientation has been shown in larvae or recently-settled individuals of other reef fishes (Mouritsen et al. 2013, Berenshtein et al. 2014). A celestial cue can be used to achieve orientation in any direction, so the fact that orientation in *C. atripectoralis* larvae differs with region does not imply that a celestial cue is not being used by the larvae of this species.

We found differences in net over-bottom movement (current plus larval behaviour) between the 3 study regions. At NGBR, we found a weak over-bottom orientation to the ESE, which on the west side of the island is toward the reef, but on the east side is away from it. At CGBR, there was no significant over-bottom orientation. At NCRL, there was a strong over-bottom orientation to the west. The local currents, in particular the tidal flows at NGBR and CGBR and the wind-driven flows at NCRL, had a strong influence on these short-term measures of movement. The combination of behaviour and currents resulted

in a clear decrease, but not prevention, of downstream dispersal at NCRL. At the 2 GBR regions, the tidal movement had a strong influence, although much of this would likely be cancelled if observations on individual larvae could be carried out over a complete tide cycle rather than for only 10 min. If the orientation behaviours we documented are a dispersal-minimizing evolutionary response to local conditions, one would not necessarily expect short-term measurements like ours to capture that minimization.

Our study provides the first clear evidence that there can be regional differences in through-water orientation by fish larvae. The differences in orientation we found would result in decreased downstream movement of larvae during their pelagic phase. Most modelling studies of larval dispersal that have attempted to include orientation behaviour have concluded that results in smaller dispersal distances than if the modelled larvae behaved passively (e.g. Armsworth 2001, Armsworth & Roughgarden 2005, Staaterman et al. 2012, Staaterman & Paris 2013). However, in most dispersal models, little of the orientation behaviour is based on empirical measures of what the larvae actually do in the ocean, and much modelled behaviour is of the sort that states 'if a larva passes within x km of any reef, it is assumed to have settled on that reef' (see Staaterman & Paris 2013 for a critique of this approach). Further, dispersal models typically make the implicit assumption that larval orientation behaviour does not vary regionally over the model universe. Modellers will now have to consider the possibility that the behaviour of their target species might be regionally variable. Our results also emphasize the difference between movement and orientation through-water and over-bottom: large differences between the two are likely, and models must take this into account (Staaterman & Paris 2013).

In the past decade, increasing evidence of the abilities and behavioural sophistication of larval marine fishes has emerged (Leis 2010, Peck et al. 2012). It is clear that the 'simplifying assumptions' of the past about the passive drift of fish larvae can no longer be justified (Staaterman & Paris 2013, Llopiz et al. 2014). In parallel with these developments has been increasing empirical evidence that larval dispersal takes place over smaller average distances than was previously thought, with significant amounts of self-recruitment (Jones et al. 2009). Modelling of larval dispersal has also increased in sophistication and increasingly requires empirical inputs on larval behaviour (Paris et al. 2007, North et al. 2009, Staaterman & Paris 2013). This study is another contribution to these developments.

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